

CALCOFI TIME SERIES: AN OVERVIEW OF FISHES

PAUL E. SMITH AND H. GEOFFREY MOSER

National Marine Fisheries Service
Southwest Fisheries Center
P.O. Box 271
La Jolla, California 92038

POPULATION PROCESSES

The stated objective of CalCOFI is "to determine what controls variations in population size and availability in oceanic fishes off the west coast of North America." The chief disciplines to be applied to this work are fishery biology—the study of population and biological community reactions to commercial harvest—and biological oceanography—the study of how the biological and physical environment affects biological populations and communities.

Murphy (1966, p. 69) concluded that the Pacific sardine was overfished and that the virtually unfished anchovy had increased to fill its niche as a regionally dominant planktivore. However, the fossil-scale record (Soutar and Isaacs 1974), which is considered to be a useful index of population size and availability, shows that precipitous declines in the Pacific sardine population between 1930 and 1960 off southern California were exceeded between 1850 and 1870, when there was no fishery, and between 1900 and 1915, when the fishery was small.

Smith (1972) reviewed the time series of sardines and anchovies as indexed by their larvae and concluded (p. 873) that the size-frequency curves of the larvae of the two species were so invariant among years that competition between the two species, if any, would most likely occur at the juvenile and prerecruit stages of either species. This was contrary to the argument of Isaacs (1965) that the recruitment of anchovy and sardine could be projected from day/night differences in the early larval stages. Smith (1972) also recommended that the ideas should be tested with surveys of larger larvae and juveniles. He pointed out that the number of batches of spawn per unit time might be plastic (Smith 1972, p. 873). This biases the indices of population size by failing to estimate the degree of interannual variation in the amount of spawning per unit time per unit of adult biomass. In this connection it was pointed out that the decline of sardine spawning in the spring and summer has coincided with an increase of spawning in spring by the anchovy. Current estimates of historical biomass (Lo 1985) indicate that apparent increase in

anchovy spawning biomass following the collapse of the sardine population could result from increased repetitive spawning as well as increased anchovy spawning biomass.

Another element in variations in population size and availability of fishes is the biological community structure. Moser et al. (1987) showed that there were major changes in mesopelagic and epipelagic fish recurrent groups during climatic changes. But data from only seven years centered on the 1957 El Niño were analyzed, so the long-term coherence of the changes cannot yet be assessed. For the same period, Colebrook (1977) showed that there were major shifts in the types of zooplankton, with particularly significant shifts in the north-south distribution of zooplankton and secondary changes in the onshore-offshore abundance.

What are the critical time and space scales for understanding the fluctuations in abundance of oceanic fishes off the North American Pacific coast? Haury et al. (1978) suggest a rationale and design:

Since the study of the causes of variation in population size is one of the chief objectives in ecological research, one reasonable approach is to select for study those scales where the variation seems to be the greatest . . . the [length scale between] . . . 50 and 1000 km and the [time scale of] . . . one half to 80 years is such a scale. This scale is remarkably similar to the one of Stommel's [time and space variation diagram] showing the most "energetic" part of the ocean. Further, it is about the size of many populations or stocks of planktivorous fish. This may not be purely coincidental.

While the Murphy (1966) proposal that the northern anchovy biomass has replaced the sardine cannot be supported by current biomass estimates of the period he studied (1932–65) or the longer period of scale-deposition rates (Soutar and Isaacs 1974), he did demonstrate an interesting coherence in spawning success rate lasting 3–5 years (Murphy 1966, p. 53). Simple population theory would suggest that a population at the carrying capacity of the environment would have an alternation of spawning success rates, and that populations over

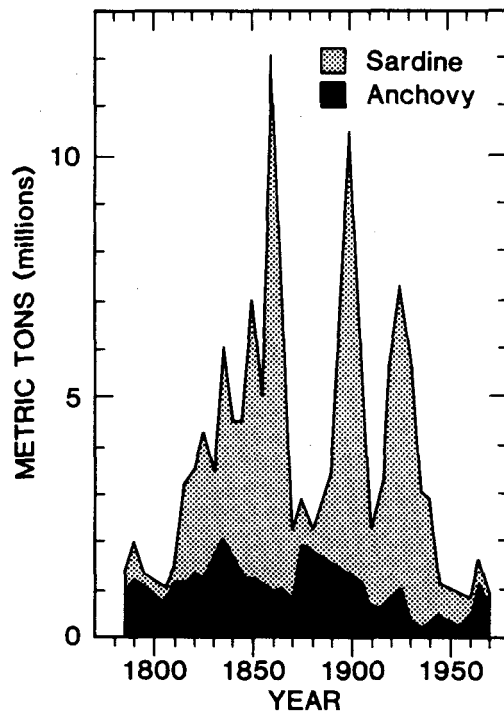


Figure 1. Revised estimate of the spawning biomass of northern anchovy between 1790 and 1970 (180 years at 5-year intervals) derived from the scale-deposition rate in two anoxic basins (Soutar and Isaacs 1974) and adjusted to the spawning biomass determined between 1980 and 1985 for northern anchovy (Methot and Lo 1987), and estimated between 1951 and 1969 (Lo 1985). The Pacific sardine biomass remains the same as in Smith 1978.

the carrying capacity would have poor spawning success. Murphy described multiyear sets of spawning success or failure as indicating population growth mediated by changes in the carrying capacity rather than as a population equilibrium about a fixed carrying capacity. In addition to the 3–5-year coherence in spawning success, there appear to be long-term trends in the sardine and anchovy populations in the scale-deposition record of Soutar and Isaacs (1974) (Figure 1).

It is the purpose of this paper to speculate on the future directions of CalCOFI field work as it relates to processes and patterns that control the variations in population size and availability of oceanic fishes. Many new opportunities are afforded by the technical advances of the last 50 years. The precision and accuracy of primary production estimates have grown steadily. Lasker (1970) specified the level of production necessary

for maintaining the Pacific sardine population. The population dynamics and energetics of several other important herbivorous and omnivorous species in the area have been elaborated. The key ecosystem boundaries, and the fauna and their temporal shifts have been described. The scientific basis for conducting ecosystem management exists for some groups of species, but there are formidable technical problems in implementing management.

How Do Population Parameters Vary in Northern Anchovy?

Population maintenance includes the processes of growth, survival, and reproduction. There is important new work on these processes for the massive local population of northern anchovy. Hunter and Leong (1981) found that northern anchovy females spawned 20 batches per year. The energy for only 2 batches was resident in the ovaries; about 13 could be formed from stored fat; the rest would therefore have to be derived from local contemporaneous primary and secondary plankton production. Smith and Eppley (1982) found that the abundance of anchovy larvae in the Southern California Bight region was positively associated with zooplankton standing stock in the previous summer and with primary production in the same quarter.

Theoretically, it is possible to specify all the variations in the northern anchovy population by knowing the variations of reproductive effort of the adults, and growth and survival of all stages (Smith 1985a). Current methods of estimating reproductive effort in anchovy do not depend on index correlations, but directly estimate the reproductive parameters (Lasker 1985, Introduction) and also allow the estimation of embryonic and larval survival. The short 6-year period for which this has been done is not adequate for time-series analysis, but it may be interesting to compare the variations in reproductive and early life-history parameters with the actual variation in spawning biomass. This 6-year period includes 2 years before and after the 1982–1983 El Niño (Chelton et al. 1982; Smith 1985b; Fiedler et al. 1986).

One can see from Table 1 that there are many variables in the reproductive process which may be responsible for a considerable fraction of the recruitment variability. In this 6-year period, the absolute recruitment in numbers of fish varied 64%. The relative recruitment rate in terms of number of recruits per ton of spawners varied 104%. The reproduction parameters varied from a low of 14%

TABLE 1
Interannual Variation of Population Parameters of the Northern
Anchovy (*Engraulis mordax*), 1980-85

Parameter	Mean	Standard deviation	coefficient of variation	Ref. *
Spawning biomass (thousand metric tons)	567	198	35%	1-6
Spawning area (naut. sq. mi.)	25,167	7,679	31%	1-6
Density (grams per sq. m.)	7	3.3	47%	1-6
Spawning female wt (grams)	14.5	3.1	21%	1-6
Specific fecundity (eggs per gram per batch)	513	71.7	14%	1-6
Batch fecundity (eggs per batch)	7,476	2,079	28%	1-6
Interval (days between batches)	8	1.7	21%	1-6
Mean age (years on Feb. 1)	1.8	0.4	23%	8
Year class (10 ⁶ fish)	51	33	64%	8
Juvenile length (mm on Oct 1)	82	7.6	9%	7
Egg production (10 ¹² eggs/day)	18	5	28%	1-6
Egg mortality (daily instantaneous)	0.24	0.09	38%	1-6
Yolk sac mortality (daily instantaneous)	0.08	0.018	22%	7
Firstfeed mortality (daily instantaneous)	0.14	0.019	14%	7
2-8 mm mortality	1.7	0.36	21%	7
8 mm larvae production (10 ¹² /day)	0.19	0.05	27%	7
Eggs to 8 mm (eggs per 8 mm)	102	35	34%	Derived from 7
Year class (thousand fish per MT of spawner)	116	121	104%	Derived from 7

*References:
1. Bindman 1986; 2. Hewitt 1985; 3. Picquelle and Hewitt 1984;
4. Picquelle and Hewitt 1983; 5. Stauffer and Charter 1982; 6. Stauffer and Picquelle 1981; 7. Fiedler et al. 1986; 8. Methot 1986.

for specific fecundity and first-feeding mortality to about 30% for egg mortality, egg production, and batch fecundity. We have not considered any environmental factors, but these internal population factors seem large enough so that combining them with unlisted factors could well account for the observed recruitment variation.

What is missing is a data set designed to partition the relative importance of controls on recruitment. In particular, it remains to be seen how the strong environmental controls interact with the weak population size controls and where in the life cycle these interactions take place. Early life stages can occasionally form part of the variation in recruitment, but much expanded work must be done to

sample late larvae and juveniles in addition to (not instead of) early larvae and embryos.

The major problems in sampling late larvae and juveniles (which have been largely solved for embryos and early larvae) are: (1) they are widespread geographically, and there is no way to detect which larvae or juveniles will eventually contribute to recruitment; (2) the late larvae and juveniles are extremely mobile and in schooled patches, thus more sophisticated samplers and more numerous samples will be needed to determine abundance of these stages; and (3) their growth rate is much more plastic than embryos and early larvae, so that regional and seasonal differences in growth rate will require many age and size determinations. In short, analysis of these late larval and juvenile stages will not add to the understanding of the entire life cycle until more money, ship time, and personnel are available for their study. Obviously, as Peterman et al. (1988) point out, the prediction of recruitment could improve as the time between the prediction and recruitment is shortened; this will come about only as it becomes economically feasible.

Another deficiency of all analyses of recruitment variability to date is the inability to assemble the sources of variability that arise from other spatial elements and in other time periods. For example, in addition to being fished, the northern anchovy is preyed upon by a wide variety of fishes, birds, marine mammals (which migrate here from the tropics and from the Arctic, thousands of miles outside the anchovy habitat), and by temperate and tropical tunas (some of which are spawned in the western Pacific 6000 miles away). Some major predators on the anchovy at different stages have life cycles of the order of weeks or months; others have life cycles of years to decades. It would not be unusual, then, for population responses to additional predation pressure on sardines or anchovies to take a decade if the population undergoing change were the northern fur seal; years if predatory populations were Pacific mackerel or one of the mesopelagic fishes; or months if the predatory population were euphausiids or copepods.

Are Time Series of Populations off California Stochastic or Coherent on Long Time Scales?

In Table 2 we have listed measures of periodicity of the fossil-scale series of Soutar and Isaacs (1974). The technique was to count and identify the scales in 5-year intervals for 190 clearly marked varves. We analyzed the time series with an integrated periodogram to determine whether the

TABLE 2
Coherence of Successive Scale Deposition Rates

	5-yr periods	Frequency ^a	Significance ^b	Period ^c
Anchovy	38	low	>0.95	50 yr
Sardine	38	low	>0.95	40 yr
Pacific hake	38	low	>0.75	65 yr
Pacific mackerel	38	low	>0.75	50 yr
Pacific saury	38	low	>0.75	30 yr
Other scales	38	low	>0.95	50 yr

^aLow frequency of change in trend equals high coherence.

^bSignificance of deviation from random in an integrated periodogram.

^cMajor period in a time series.

series deviated from the random on the low-frequency or high-frequency side and to determine the significance of the cumulative deviation. Each time series was categorized as low-frequency if all periods were above white noise. If they were below the 0.75 probability line the time series was labeled < 0.75; if the series was between the 0.75 and 0.95 probability lines the time series was labeled < 0.95; and if the series projected above the 0.95 line the series was labeled > 0.95. The period was chosen from the maximum peak (10 sample units = 50 years) on the periodogram when there was more than one peak.

We can see from Table 2 that there is major agreement among the species as to the spectral composition of the time series. To varying degrees of significance, the spectrum is of low frequency. The period of change is long, ranging from 30 years in the Pacific saury to 65 years in the Pacific hake. One may assume that the mechanism is environmental, because the generation time of these species is always less than 10 years. In addition to the 3–5-year scale detected in spawning success of sardine (Murphy 1966), we must now be alert to mechanisms operating on a much longer scale. In particular, for management purposes we will need criteria for determining changes in regime from periods of successful reproduction to unsuccessful reproduction.

How Do the Time Series of the Species Compare from Two Collection Sites 1000 km Apart?

Soutar and Isaacs (1974) reported two time series, one from the Santa Barbara Basin at 34°N and one from the Soledad Basin at 26°N. We examined cross-correlations with lags from –5 to 5 representing a period of 55 years. In Table 3 we have the correlation coefficient at the 0 lag or contemporaneously. We have also listed the minimum and maximum cross-correlation coefficients with the lag at which this was achieved.

TABLE 3
Comparison of Cross-Correlation between the Scale-Deposition Time Series at the Santa Barbara Basin and the Soledad Basin (1000 km Southeast)

	Zero lag R	Min R	Lag	Max R	Lag
Northern anchovy	0.26	–0.28	5	0.43	–3
Pacific sardine	–0.02	–0.21	–3	0.24	1
Pacific hake	–0.17	–0.37	–4	0.50	5
Pacific mackerel	0.37	–0.15	–5	0.57	–1
Pacific saury	0.65	–0.09	2	0.66	–1
Other	0.03	–0.33	–5	0.18	1

The Pacific saury, with a transpacific distribution, shows the most cross-correlation between these sites 1000 km apart. The Pacific sardine shows the least. One may conclude from this that the relationships between the sites are generally weak. This could be interpreted to mean that the tendency for these populations to range north and south with long-term changes in climate is nil and that population changes at one site are neither in phase nor out of phase with populations at the other site.

At a Scale-Deposition Site, Do Population Trends of the Major Species Show Interactions Affecting Population Abundance?

To what degree do these populations change at the two sites in response to one another? Table 4 for the Santa Barbara Basin scales and Table 5 for the Soledad Basin scales list the zero-lag correlation coefficients, the minimum cross-correlation coefficient and its lag, and the maximum cross-correlation coefficient and its lag. Here again, as in the species comparisons between basins, most of the correlation coefficients are low. This suggests that within the scale-deposition area of a basin the population densities of the species are unrelated. Some exceptions at the Santa Barbara Basin include the zero-lag (same 5-year period) correlation of 0.66 between the anchovy and hake populations. This means that 40% of the biomass series of either species is controlled by the other or by a common environmental factor. The correlation coefficient between Pacific mackerel and Pacific saury is 0.65 with a lag of 3 (15 years). The largest negative influence is between the northern anchovy and Pacific mackerel at –0.43 with a lag of –1. This suggests that a high biomass of Pacific mackerel is followed in the next 5-year period by a low biomass of anchovy; however, the control is low (about 20%).

At the Soledad Basin there appears to be a bit more structure among the species. Here the an-

TABLE 4
Cross-Correlation Coefficients among Several Species at the Santa Barbara Basin Site

	Pacific sardine	Pacific hake	Pacific mackerel	Pacific saury	Other
No lag					
Northern anchovy	0.33	0.66	-0.36	-0.38	0.03
Pacific sardine		0.38	-0.06	-0.26	-0.21
Pacific hake			-0.18	-0.24	0.01
Pacific mackerel				0.14	-0.11
Pacific saury					0.24
Minimum (lag)					
Northern anchovy	-0.02(-2)	-0.02(-5)	-0.43(-1)	-0.45(1)	-0.19(4)
Pacific sardine		-0.29(4)	-0.35(-4)	-0.31(-2)	-0.29(-2)
Pacific hake			-0.36(-5)	-0.34(-1)	-0.40(4)
Pacific mackerel				-0.19(-3)	-0.33(-4)
Pacific saury					-0.21(-4)
Maximum (lag)					
Northern anchovy	0.41(4)	0.66(0)	0.17(2)	0.04(5)	0.36(-5)
Pacific sardine		0.46(-1)	0.14(2)	0.13(5)	0.18(4)
Pacific hake			0.25(5)	-0.01(-5)	0.53(-4)
Pacific mackerel				0.65(3)	0.18(1)
Pacific saury					0.24(0)

Analysis of data from Soutar and Isaacs 1974.

chovy and hake are negatively correlated at all lags. The correlation is most negative at -1 lag ($r = -0.50$), and it is generally the same at zero lag (-0.45). Sardines are positively correlated with Pacific mackerel ($r = 0.68$, lag 2) and Pacific saury ($r = 0.79$, lag 3). Pacific mackerel is also positively correlated with Pacific saury ($r = 0.64$, lag 1). Anchovy is positively correlated at all lags with the category "other" scales, with a maximum correla-

tion of 0.81 at 0 lag. Hake is also correlated negatively ($r = -0.56$) with "other" scales at a lag of -2 in the Soledad Basin area.

From this analysis, it appears that controls of fish populations on each other are weak, and common responses to environmental changes are similarly weak. Thus although Murphy (1966), Lasker (1970), and Smith and Eppley (1982) all agree that the major pelagic schooling stock, either sardine

TABLE 5
Cross-Correlation Coefficients among Several Species at the Soledad Basin Site

	Pacific sardine	Pacific hake	Pacific mackerel	Pacific saury	Other
No lag					
Northern anchovy	-0.26	-0.45	-0.19	-0.29	0.81
Pacific sardine		0.24	0.38	-0.10	-0.22
Pacific hake			0.44	0.33	-0.22
Pacific mackerel				0.31	-0.19
Pacific saury					-0.17
Minimum (lag)					
Northern anchovy	-0.33(-5)	-0.50(-1)	-0.35(-3)	-0.34(3)	0.11(5)
Pacific sardine		-0.24(-5)	-0.25(-5)	-0.21(-4)	-0.33(-4)
Pacific hake			-0.11(-3)	-0.18(-5)	-0.56(-2)
Pacific mackerel				-0.15(-4)	-0.35(3)
Pacific saury					-0.31(-3)
Maximum (lag)					
Northern anchovy	-0.13(-2)	-0.17(5)	-0.18(1)	0.00(-5)	0.81(0)
Pacific sardine		0.46(-2)	0.68(2)	0.79(3)	-0.12(-2)
Pacific hake			0.44(0)	0.47(1)	-0.06(5)
Pacific mackerel				0.64(1)	-0.06(5)
Pacific saury					-0.01(4)

Analysis of data from Soutar and Isaacs 1974.

or anchovy, is a massive consumer of production relative to the total produced in the California Current system, there does not seem to be any evidence from the fossil-scale record that they compete within a habitat or migrate from one end of the habitat to another. Competition, if any, must be part of a vast and changing array of as yet unmeasured population controls on the major species. It seems possible that abundant mesopelagic populations which migrate to the epipelagic zone and are piscivorous and planktivorous could exert predatory control on the larvae and juveniles of the common epipelagic fishes.

COMMUNITY PROCESSES

The work of Scofield (1934) revealed that the sardine spawned throughout a large proportion of the California Current region, and this was confirmed by Ahlstrom (1948) during the beginnings of the CalCOFI program. Thus a plankton survey designed to comprehensively sample sardine spawning had the potential to yield biogeographic information on a large array of marine organisms. This potential was realized only through the research efforts of dedicated scientists.

Dr. Elbert Ahlstrom was in charge of ichthyoplankton, and from the beginning was determined to identify each sample as far as his knowledge would allow. This knowledge grew rapidly; he soon became preeminent among the small group of people working on ichthyoplankton around the world. Thus, while the primary focus was on the early life history of the sardine and later its relation to the anchovy (Ahlstrom 1966), he was steadily building a fund of information on the ontogeny, systematics, and biogeography of eastern Pacific fishes. His series of definitive papers on early life history and his active role in training and guiding young researchers were principal factors in building a once modest group of devotees into a major field of ocean science. His contributions to the ontogeny and systematics of fishes culminated in an international symposium and a book that summarized and integrated the existing knowledge of these fields (Moser et al. 1984).

The patterns of distribution and abundance of larvae of the principal fish taxa in the California Current and adjoining regions have been reported by Ahlstrom and his co-workers in the CalCOFI Atlas series (Ahlstrom 1969, 1972a; Ahlstrom and Moser 1975; Ahlstrom et al. 1978; Kramer 1970; Kramer and Ahlstrom 1968; Hewitt 1980) and in individual research papers (Ahlstrom 1961, 1965, 1971, 1972b; Ahlstrom and Ball 1954; Ahlstrom

and Counts 1955, 1958; Ahlstrom and Stevens 1977; Ahlstrom et al. 1976; Ambrose et al. 1983; D'Vincent et al. 1980; Kramer 1960; Loeb et al. 1983a, b, c; Moser and Ahlstrom 1970; Moser et al. 1973, 1977, 1983, 1986; Stevens and Moser 1982; Sumida et al. 1979, 1985). Lack of a computer data base for CalCOFI has limited our ability to analyze the time series. Since 1983 (Charter et al. 1986¹) we have been working to remedy this and in the near future will publish 23 ichthyoplankton data reports covering CalCOFI surveys from 1951 to 1981 (see Appendix); the computer data base will be made available to the public through the on-line system described by Roger Hewitt in this volume.

Concurrently with the development of the data base, we have begun to analyze the larval fish assemblages of the California Current region. The northern anchovy, *Engraulis mordax*, has increased in relative abundance throughout the three decades from 1951 to 1981 and accounts for about half the larvae collected over this span (Table 6). Next most numerous are three taxa that consistently rank 2d, 3d, or 4th through this time span: the Pacific hake (*Merluccius productus*), the eastern tropical Pacific gonostomatid *Vinciguerria luccetta*, and the rockfish genus *Sebastes*, which includes over 70 species in the survey area. These 4 top-ranking species represent 72% of all larvae taken. Next in overall rank are 3 midwater species: the deepsea smelt *Leuroglossus stilbius* and two mesopelagic lanternfish, *Triphoturus mexicanus* and *Stenobrachius leucopsarus*. Eighth in overall rank is the sanddab genus *Citharichthys*, which includes 6 species in the CalCOFI region. The remaining 2 species in the top 10 are the Pacific sardine (*Sardinops sagax*) and the jack mackerel (*Trachurus symmetricus*), both of which have shown a relative decline throughout the time series.

The faunal affinities of these top-ranking taxa reflect the transitional nature of the CalCOFI region. Congeners of the anchovy, sardine, jack mackerel, and hake are also abundant in the three other eastern boundary currents of the Pacific and Atlantic. *S. leucopsarus* is a subarctic-transitional species, and *L. stilbius* has a transitional distribution, *sensu* Johnson and Brinton (1965), extending northward from the California Current across the Pacific in a narrow zone between the subarctic and central water masses. *Sebastes* is a subarctic-tran-

¹Charter, R., D. A. Ambrose, H. G. Moser, E. M. Sandknop, P. E. Smith, E. G. Stevens and B. Y. Sumida. The CalCOFI ichthyoplankton data base and data reports. Poster presented at CalCOFI Annual Conference, Lake Arrowhead, California, October 21-23, 1986.

TABLE 6
Relative Abundance of the 10 Top-Ranking Larval Fish Taxa Taken on CalCOFI Cruises, Shown as Standardized Counts Pooled for Each Decade

Taxon	1951-81			1951-59			1960-69			1972-78			1980-81		
	Rank	Count	Percent	Rank	Count	Percent	Rank	Count	Percent	Rank	Count	Percent	Rank	Count	Percent
<i>Engraulis mordax</i>	1	5,645,276	49.0	1	1,195,566	33.0	1	2,473,787	54.0	1	1,491,654	57.7	1	484,269	65.5
<i>Merluccius productus</i>	2	1,014,627	8.8	2	523,588	14.4	3	268,044	5.9	2	204,259	7.9	5	18,736	2.5
<i>Vinciguerria lucetia</i>	3	905,814	7.9	3	335,862	9.3	2	384,025	8.4	4	149,191	5.8	3	36,736	5.0
<i>Sebastes</i> spp.	4	718,841	6.2	4	251,065	6.9	4	259,938	5.7	3	157,430	6.1	2	50,408	6.8
<i>Leuroglossus stilbius</i>	5	444,399	3.9	5	176,671	4.9	6	165,733	3.6	5	76,312	3.0	4	25,683	3.5
<i>Triphoturus mexicanus</i>	6	396,178	3.4	6	165,238	4.6	5	170,755	3.7	8	47,799	1.8	7	12,386	1.7
<i>Stenobrachius leucopsarus</i>	7	313,131	2.7	8	132,683	3.7	7	104,316	2.3	6	60,492	2.3	6	15,640	2.1
<i>Citharichthys</i> spp.	8	275,176	2.4	9	128,342	3.5	8	81,621	1.8	7	56,498	2.2	8	8,715	1.2
<i>Sardinops sagax</i>	9	218,722	1.9	7	136,883	3.8	10	62,845	1.4	16	12,946	0.5	13	6,048	0.8
<i>Trachurus symmetricus</i>	10	206,235	1.8	10	116,148	3.2	9	69,959	1.5	14	16,115	0.6	14	4,013	0.5
			87.9			87.3			88.3			87.9			89.6
All taxa		11,532,013			3,628,396			4,578,555			2,586,250			738,812	
No. stations		30,296			14,025			11,256			4,037			978	

sitional shorefish group, and the various species of *Citharichthys* are found in coastal waters from the subarctic through the tropics. *T. mexicanus* is a subtropical species abundant in the southern reaches of the California Current, and *V. lucetia* is an eastern tropical Pacific species. Central water mass species are not abundant in the CalCOFI samples; however, warm-water cosmopolites such as the myctophids *Diogenichthys atlanticus*, *Hygophum reinhardtii*, and *Myctophum nitidulum* appear where central water impinges on the California Current off southern California and Baja California. The distributional patterns of the principal and less-abundant larval fish taxa in the CalCOFI region are closely tied to water masses, clearly affirming what has been shown for a wide array of zooplankton species (Reid et al. 1978).

As a first step in studying potential environmental effects and species interactions, we performed a recurrent group analysis on the 7-year span of the time series from 1954 to 1960 (Moser et al. 1987). This period was chosen because there was maximum areal and seasonal sampling coverage during a sequence of anomalously cold and warm oceanographic regimes. Also, initial identifications of the samples were fairly reliable, and these were improved during the editing and verification of the data base. The recurrent group method identifies groups of taxa that occur together frequently and are consistently part of each other's environment. This method tends to avoid potential misinterpretations that can arise from abundance analyses of patchy organisms.

Analysis of nearly 200 taxa from the composite 7-year data set produced 9 recurrent groups formed by 30 taxa. Intergroup affinities produced two large complexes of 4 recurrent groups each.

We refer to these as the "northern" and "southern" complexes, since their constituents had primarily warm- or cold-water taxa or were linked to warm- or cold-water taxa through affinity indices. Spawning was seasonal in most species, with winter or spring maxima in the northern complex and spring or summer maxima in the southern complex. Each complex consisted of a 5-member group with strong connections to the smaller groups in the complex.

The large group in the northern complex was a mix of abundant subarctic-transitional (*L. stilbius*, *S. leucopsarus*, *Sebastes* spp.) and transitional (*M. productus*, *Bathylagus ochotensis*) taxa, which were strongly interlinked with *E. mordax* and *S. sagax* in two other groups. In contrast to the northern and coastal nature of this complex, the southern complex comprised primarily mesopelagic species that inhabit more southerly and offshore waters. The 5-member group included transitional species (*Bathylagus wesethi*, *Lampanyctus ritteri*, *Symbolophorus californiensis*) and warm-water cosmopolites (*Cyclothone* spp., *Diogenichthys atlanticus*) that were strongly linked to an eastern tropical Pacific group (*V. lucetia*, *Diogenichthys lateratus*, *Hygophum atratum*, *Goniichthys tenuiculus*) and a group comprising transitional (*Trachurus symmetricus*, *Protomyctophum crockeri*) and subtropical (*T. mexicanus*) species. A third complex was associated with the extensive coastal shelf region of central Baja California and consisted of a group of four subtropical shorefish taxa.

The structure and composition of the groups varied in analyses of individual years, more so in the southern complex; however, the northern and southern complexes were generally conserved. The two complexes were linked by a single pairing

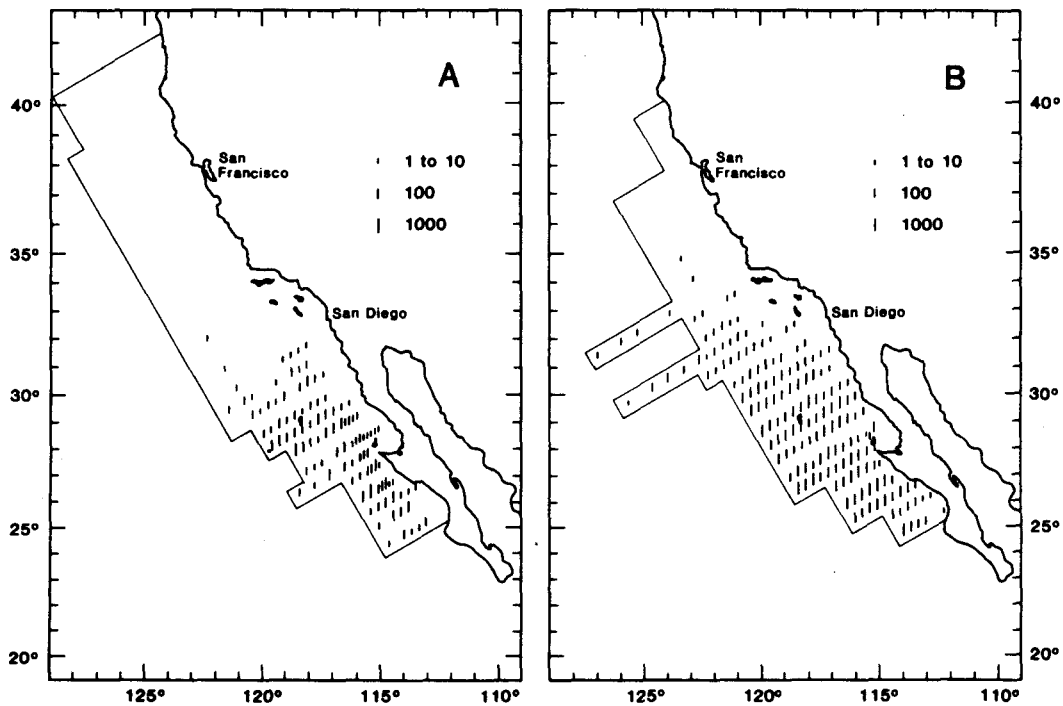


Figure 2. Change in distribution of larvae of *Vinciguerria lucatia* during cold (A) and warm (B) temperature regimes in the California Current region. Pooled numbers of larvae for three cold years (1954-56) and three warm years (1958-60) are indicated by exponentially scaled bars. The survey pattern for each series of years is outlined.

(*E. mordax*-*T. mexicanus*) in the composite analysis, although in some years the links between the two complexes were stronger and more numerous, and there was some switching of group members between complexes. Where this occurred, the southern complex group of *T. mexicanus*-*P. crockeri*-*T. symmetricus* and the northern complex group of *E. mordax*-*Citharichthys* were usually involved, emphasizing the transitional position of these taxa in the CalCOFI region.

Variation in the structure and composition of the complexes and their constituent groups was, in part, related to the major oceanographic changes that occurred during 1954-1960. Conditions in the first half of the 1950s were generally cool, culminating in the strong negative temperature anomaly during 1956. A warming trend began in 1957, leading to a major El Niño event in 1958 and 1959. Mixed-layer isotherms were shifted northward more than 200 km, shifting the distribution and abundance of some larval fish taxa northward, (Figure 2) and causing the above-mentioned

changes in recurrent groups. These changes were not as great as those associated with the anomalously cold year of 1956, when affinity indices were lowered among southern complex species, and recurrent groups in this complex were markedly depauperate (see Moser et al. 1987 for details).

From this brief summary it is clear that the CalCOFI surveys reveal the major faunal associations and broadscale environmental interactions in the California Current region. This was particularly true for the 1950s, when monthly sample coverage extended over the full length of the pattern. Biogeographic information has diminished since 1960, with the areal and temporal shrinkage of the survey pattern; however, even the present minimal quarterly coverage of the Southern California Bight is sensitive to changes in ocean regimes because subtropical, eastern tropical Pacific, and central water mass species expand their spawning boundaries into this region. The original extensive coverage was also essential in defining the broad spawning ranges of commercial species such as Pa-

cific hake, jack mackerel, Pacific mackerel, and the rockfishes. Fishery scientists have relied heavily on CalCOFI data in developing the knowledge required to manage these populations.

The early surveys also showed that many important coastal recreational and commercial species spawn off Baja California. Ocean whitefish (*Caulolatilus princeps*) appears to spawn exclusively off Baja California, since larvae have not been taken north of the Mexican border (Moser et al. 1986). White seabass (*Atractoscion nobilis*), yellowtail (*Seriola lalandi*), and bonito (*Sarda chiliensis*) spawn primarily off Baja California, with small numbers of larvae appearing off southern California (Moser et al. 1983; Sumida et al. 1985; original data). Barracuda (*Sphyræna argentea*) and California halibut (*Paralichthys californicus*) spawn off southern California, but the greater part of their spawning range extends the entire length of Baja California (Kramer and Smith 1973). Recruitment of these transboundary stocks to southern California is either dependent on or strongly influenced by stocks off Mexico. The United States and Mexico are highly interdependent in the use and management of these stocks, and if CalCOFI is to be involved in studies of their production and recruitment, the present survey pattern will have to be expanded south of the Southern California Bight.

During the past ten years there has been increased ichthyoplankton research on shorefish populations, primarily because of potential impacts of power plants and urban development (Brewer et al. 1981; Gruber et al. 1982; Schlotterbeck and Connally 1982; Barnett et al. 1984; Lavenberg et al. 1986; Walker et al. 1987). These workers have used CalCOFI ichthyoplankton techniques to study the zone between the most shoreward CalCOFI stations and the beach. One of their key findings is a distinct nearshore ichthyoplankton fauna, which peaks at about 40-m bottom depth and is poorly sampled at the most shoreward CalCOFI stations. Many of these species settle to the bottom at early larval stages, apparently as an adaptation to remain nearshore, and there is a general tendency in these larvae to move downward and shoreward ontogenetically. Some species are neustonic and may be transported shoreward in surface slicks associated with tidally forced internal waves (Shanks 1983). Larvae of the nearshore assemblage are comparatively rare in CalCOFI samples, generally occur well seaward of their zone of settlement, and may represent reproductive wastage rather than potential recruits. Alternatively, they may possess behavioral mechanisms that al-

low far-ranging planktonic stages to recruit to the nearshore habitats of the adults. This question can be addressed by analyzing the CalCOFI and nearshore ichthyoplankton data bases that are presently being assembled, but it probably cannot be answered without concentrated field surveys in the transition region between the two zones.

An initial objective of the CalCOFI program was to determine the environmental and biotic factors that affect production, recruitment, and population fluctuations of the sardine. During the past 40 years the program has provided spawning biomass indices of the sardine, anchovy, and mackerels (Ahlstrom 1966; Smith 1972; Parrish and MacCall 1978; MacCall and Stauffer 1983) and has documented the continued decline of the sardine and concomitant increase of anchovy in the CalCOFI region. A recent modification of CalCOFI sampling design has allowed direct estimation of anchovy and sardine spawning biomass (Lasker 1985; Wolf et al. 1987). CalCOFI has been the foundation for a number of hypotheses: sardine-anchovy competitive exclusion (Murphy 1966; Ahlstrom 1967; Isaacs 1965); ocean transport-larval survival (Parrish et al. 1981; Simpson 1987); Lasker's (1975) stable ocean-larval survival hypothesis; and MacCall's density-dependent habitat selection model (MacCall 1980; Lasker and MacCall 1983). Correlation techniques support Lasker's hypothesis that wind-driven turbulent mixing increases mortality of early-stage anchovy larvae by dissipating food patches (Peterman and Bradford 1987) but do not support the hypothesis (Lasker 1981) that recruitment and year-class strength are determined by mortality of early-stage larvae (Peterman et al. 1988). The latter authors suggested that recruitment variability would depend on survival during the late larval-prerecruit stages, which are virtually absent from CalCOFI samples.

Our research on interannual variation of incidence and abundance of CalCOFI ichthyoplankton (Moser et al. 1987) suggests that a multispecies approach might provide recruitment information on species such as sardine and anchovy. These species co-occur and interact with a wide array of other species during each life-history stage. Dominant mesopelagic species (Table 6) are not sampled by fisheries, and CalCOFI provides the only synoptic sampling of their populations. Our interpretation of the conclusions of Peterman et al. (1987) emphasizes predation during the late larval and prerecruit stages as a major determinant of recruitment. This occurs widely in the complex species

assemblages sampled by CalCOFI surveys, and its relation to recruitment may be revealed by our correlation analyses in progress.

CONCLUSIONS

The early decades of biological oceanography in CalCOFI were marked by the identification of the oceanic regions and currents that impinged on the California coastal area. Johnson and Brinton (1965) used physical oceanography and analysis of planktonic species to describe the primary boundaries. The time series of the major epipelagic fish species—sardine and anchovy—by Murphy (1966) and Soutar and Isaacs (1974) have drawn attention to two scales of change: one at the scale of 3–5 years and another that acts over periods of 3–6 decades. Recent analyses of species assemblages (Moser et al. 1987) will offer time series comparisons for additional species at the decadal scale when the analyses under way are complete. In summary:

1. Spectral analysis of the fish-scale record indicates long-lasting population trends in sardine and anchovy and does not suggest equilibrium phenomena as population controls; the period of change is of the order of a half-century for several pelagic species.
2. The reproductive parameters of the northern anchovy show variations that are much less than the variations in specific recruitment rate.
3. Scale-deposition indices at two sites separated by 1000 km show little agreement, suggesting that the critical spatial scale of the events leading to species biomass changes is less than 1000 km.
4. Species biomass interactions among the major fish populations are weak at both scale-deposition sites.
5. Analysis of fish species assemblages suggests that predation by major mesopelagic species of the California Current region could affect survival rates of ontogenetic stages of epipelagic populations (e.g., sardine and anchovy) and thus influence recruitment variations.

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Over a dozen species of euphausiids from various parts of the world are known to appear in similar aggregations at the sea surface during the day (Komaki, 1967; Mauchline, 1980), but the frequency of swarming varies from species to species. *Euphausia superba* of the Antarctic may swarm at the surface during the day throughout most of its life cycle (Marr, 1962) and is the best studied euphausiid; other species, such as *T. spinifera*, appear to swarm only seasonally or intermittently (Mauchline, 1980). The mechanism that brings about the formation of these swarms is not clear and may differ according to species. Theories proposed to account for daytime surface swarming of various euphausiid species generally fall into the following categories: (1) the animals actively congregate at the surface for some biological purpose—to feed (Paulsen, 1909; Brown et al., 1979), reproduce (Ponomareva, 1966; Mauchline, 1980; Nicol, 1984a; Endo, 1984; Endo et al., 1985) or escape predators (Komaki, 1967); (2) they are passively transported to the surface by water currents or turbulence (Aitken, 1960; Forsyth and Jones, 1966; Brown et al., 1979; Terazaki, 1980); or (3) a breakdown of an environmental barrier, such as the thermocline, enables them to expand their vertical distribution to the surface (Komaki, 1967; Endo, 1984). These theories have proven difficult to substantiate since many aspects of the swarming phenomenon are not open to experimental investigation. Also, existing published accounts lack direct hydrographic evidence and comparative information on the vertical distribution of various components of the population before, during and after swarm activity.

It is not known which of the above factors are implicated in *T. spinifera* swarming activity, but the dominance of spent females in swarms that washed ashore in southern California (Boden et al., 1955) and Oregon (Percy and Hosie, 1985) suggests that swarming may be related to reproduction. In the more northern part of its range in subarctic waters, this species is reported to have a 2-year life cycle, reaching sexual maturity in its second year, with a one-time breeding season (Nemoto, 1957). Males must transfer a pair of spherical spermatophore packets to females for fertilization to take place, and in members of this genus, females shed their fertilized eggs freely in the water (Boden et al., 1955). The length of time between spermatophore transfer and release of eggs is not known.

The goal of the present study was to identify factors associated with swarming of *T. spinifera* off central California. We made observations of swarms and associated biological activity in a swarm area, collected oceanographic information, and examined samples from individual swarm patches and plankton collections obtained before, during and after swarm activity. In this paper, we describe our results and discuss the possible adaptive significance of swarming in this species.

MATERIALS AND METHODS

Swarms were observed and sampled between 1300 and 1530 h on 31 May 1985 in the Gulf of the Farallones (37°48.3'N, 122°56.3'W). Individual patches were sampled using a hand-held dip net (mouth area = 0.1 m², mesh width = 1.0 mm). Each sample came from a discrete patch, the size of which was estimated visually. These samples were then preserved in 10% neutralized formalin and seawater. Water temperature profiles were obtained with an expendable bathythermograph (XBT).

We were able to obtain depth-stratified plankton samples in the swarm area before, during, and after surface swarm activity. This was possible because the swarms occurred in the same area (within 1.5 km) in which we had been monitoring *T. spinifera* springtime relative abundance since 1983. A set of horizontal tows of 15-min duration was made at the swarm site 12 h prior to and 12 and 24 h after swarm activity was observed. Each set consisted of tows made at 55, 37, and 18 m over bottom depths of 68–70 m. During the day of swarm activity, one tow at 55 m was completed while dipnet samples were being collected from surface waters. These collections were made with an opening-closing Tucker net (described by Hopkins et al., 1973) with an effective mouth opening of 1 m² and a mesh size of 0.335 mm. The net was towed at 1.3 m sec⁻¹. Controlled test runs using a digital flowmeter in the mouth of the net indicated this procedure strained roughly 74 m³ of water per minute, assuming

Table 1. Sex ratios, χ -square values, and significance levels of *Thysanoessa spinifera* swarm patch samples collected by dip net from the sea surface

Patch sample number	Patch area (m ²)	N	% Females	χ^2	P
1	1.0	239	0.30	38.56	<0.01
2	1.5	136	0.31	19.12	<0.01
3	4.0	147	0.12	85.34	<0.01
4	1.5	133	0.38	6.76	<0.01
5	2.0	167	0.50	0.00	N.S.
6	3.0	154	0.65	13.16	<0.01
7	2.0	179	0.55	1.82	N.S.
8	5.0	116	0.76	30.02	<0.01
9	1.0	33	0.64	1.94	N.S.

the absence of net clogging. Organism counts were standardized for 1,000 m³ of water strained by the net.

Swarm samples containing 200 euphausiids or less were examined in their entirety; larger samples were divided with a Folsom plankton splitter. Total length was measured to the nearest millimeter from the tip of the rostrum to the tip of the telson. Body length, from the base of the eye to the junction of abdomen and telson, was also measured to allow comparison with other data. These lengths were highly correlated ($r^2 = 0.957$, $P < 0.0001$). A least-squares fit of 1,304 comparisons gave the equation

$$Y = 0.742X + 0.26$$

where Y = body length and X = total length. An analysis of variance showed that variation due to regression is significant, and therefore the true slope differs from zero ($F = 29.051$; $df = 1, 1302$; $P < 0.001$). Females were classified as (1) with spermatophores attached, with ripe or ripening eggs (0.2–0.4 mm in diameter); (2) without spermatophores, with ripe or ripening eggs; (3) without spermatophores, with early developing eggs (<0.2 mm); and (4) with spermatophores attached, but with no eggs discernible in the thoracic cavity (spent). Females with spermatophores attached to the thelycum will be termed "fertilized," even though actual fertilization of eggs may not take place at the time of spermatophore transfer. Males were classified as (1) with ripe spermatophores protruding or internal; and (2) without ripe spermatophores. All specimens were grossly examined for the presence of parasites. In addition, the ventral food basket between the thoracic appendages of each specimen was examined, and contents of food boluses were identified to the lowest possible taxonomical level.

RESULTS

Nine patches, 1–5 m² in size (Table 1), each approximately 137 m apart, were sampled over an area of about 1 km². The aggregations occurred from the surface to a maximum depth of about 37 m in 71 m of water, based on echosounder readings (Fig. 1A).

Weather and sea conditions at the swarm site were seasonally mild: wind speed = 8 knots, wind direction = 270°, sea state = 2 on Beaufort scale, swell height = 1 m, swell direction = 255° mag., cloud cover = 2 (1/8 sky covered). During the cruise period (30 May–5 June), oceanographic conditions were characterized as transitional, marked by persistent south winds, relaxation of upwelling, and warming and stratification of upper surface layers.¹ Coastal Upwelling Index values (Bakun, 1975) for the central California coast were well below average for the last week in May, indicating an absence of strong upwelling during and preceding swarm activity.²

Observations of swimming behavior and patch shape were made while the ship

¹ K. Briggs, University of Santa Cruz, Santa Cruz, CA 95064, pers. commun. June 1985.

² Andrew Bakun, Pacific Fisheries Environmental Group, National Marine Fisheries Service, NOAA, Monterey, CA 93942. Unpubl. data.